

An Examination of the Relationships Between Extant *Dolomena* Wenz, 1940, *Doxander* Wenz, 1940, *Mirabilistrombus* Kronenberg, 1998, *Neodilatilabrum* Dekkers, 2008 and *Labiostrombus* Oostingh, 1925 (Stromboidea: Neostromboidae: Strombidae)

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ABSTRACT This paper presents an examination of the relationships between *Dolomena*, *Doxander*, *Mirabilistrombus*, *Neodilatilabrum* and *Labiostrombus* using character state analysis and maximum parsimony. Hypothesized relationships are presented through the introduction of definitions that bridge the understanding of the evolutionary relationships with the applied nomenclature. Dolomenini is introduced to incorporate two new subtribes: Dolomenina which combines parts of *Dolomena* ex Abbott (1960) and *Labiostrombus*; and Doxanderina, which encloses *Doxander* and *Neodilatilabrum*. Based on the generated phylogeny, *Amabiliplicatus*, *Pacificus* and *Dominus* are introduced, while *Ministrombus* is validated as monophyletic. The clustering of *Neodilatilabrum* and *Doxander* within Doxanderina, and the nesting of *Labiostrombus* within the Dolomenini are major revisions to Stromboid systematics.

KEY WORDS Character State, Gastropoda, Mollusca, Doxanderina, Dolomenini PhyloCode

INTRODUCTION

The process of ordering nature is one of continual revision and change, especially when a great many new taxa are circumscribed within a small complex of organisms, or groups have been subjected to taxonomic inflation. Many of the discrete complexes that Abbott (1960) recognised 60 years ago within Strombidae Rafinesque, 1815 have been inflated, and now stand alone as independent genera. Notwithstanding the elevation of these subgenera, the relationship between these taxonomic entities has yet to be tested. Recent revisions that have targeted stromboids have mainly focused on the circumscription of new taxa (Man in't Veld and Visser 1993; Willan 2000; Visser & Man in't Veld 2005; Liverani

2013; Thach 2016), or the revaluation of existing genera (Bandel 2007; Dekkers 2008, 2010). Yet fundamentally, there have been few attempts at determining the phylogenetic relationships between these stromboid taxa. Where resolution has been attempted, there has been no attempt to impart the cladistic findings to the practical way nature is perceived, that is in the nomenclature (Latiolais *et al.* 2006).

Dolomena Wenz, 1940, *Doxander* Wenz, 1940 and *Labiostrombus* Oostingh, 1925 were once considered subgenera of *Strombus* Rafinesque, 1815, but have now all been elevated to genera. The elevation of these taxa, and the circumscription of new genera such as *Margistrombus* Bandel, 2007 (= *Neodilatilabrum* Dekkers, 2008), rather than as

subgenera within *Dolomena*, has resulted on the loss of the overarching relational meaning. Meaning that was once contained in the nomenclature and evidenced as a consequence of rank or subordinate taxa relationships before the age of taxonomic inflation of the subordinate ranks, particularly well-illustrated in the shift of subgenera to genera in Strombidae.

Dolomena are all medium-sized, distributed throughout the Indo-Pacific, and with their maximum diversity centred in the coral triangle. While these groups have also undergone a continual process of accretion into the genus *Dolomena* due to new circumscriptions of taxa, there has been no attempt at deciphering the relationships between taxa apart from the gross morphological similarity used only in the context of discriminating taxa (Man in't Veld and Visser 1993; Willan 2000; Visser & Man in't Veld 2005; Liverani 2013; Thach 2016). The presently assigned taxa to *Dolomena* still largely follow the historical arrangements outlined in Abbott (1960), although some species were later assigned to new genera such as *Neodilatilabrum* recognizing some of the natural divisions of Abbott (1960). Abbott (1960) arranged these taxa in a logical order based on similarity in shell characters: *Strombus plicatus* (Röding, 1798) complex (extant species pp. 89 – 92; extinct species p. 92- 93); *Strombus dilatatus* Swainson, 1821 complex (extant species pp. 93-94; extinct species pp. 95); *Strombus labiosus* Wood, 1828 complex (extant species 95-97; extinct species p. 97); *Strombus marginatus* Linnaeus, 1758 complex (extant species pp. 97-102; extinct species pp. 102 – 103); and the *Strombus variabilis* Swainson, 1820 grouping which includes *Strombus minimus* Linnaeus, 1771 (extant species 103-106; extinct species: none). However, Abbott (1960) presents no clear methodological approach to understanding the relationships

between the taxa he linked together, nor presented any justification other than similarity in form for his species justification. This led to a gross over simplification of the diversity presented before him (Maxwell *et al.* 2019a, b). Therefore, we aimed to bring a higher level of resolution of the genera and their relationships within the Strombidae using phylogenetic relationships to demonstrate that nomenclature can reflect the current evolutionary understanding within that complex rather than the simple aggregation of taxa based on uncritical analysis of form alone.

ABBREVIATIONS

SMC – Stephen Maxwell Collection, Cairns, Queensland, Australia.

AMD – Aart Marius Dekkers Collection, Purmerend, the Netherlands.

METHODS

The target taxa of this study were the members of the *Dolomena* Wenz, 1940 ex Abbott (1960) complex and the newly circumscribed taxa ascribed to that genera and its modern derivatives. *Laevistrombus* Abbott, 1960 (*Laevistrombus vanikorensis* (Quoy & Gaimard, 1834)), *Mirabilistrombus* Kronenberg, 1998 (*Mirabilistrombus listeri* (Gray, 1852)), *Doxander* (*Doxander vittatus* (Linnaeus, 1758)) and the monotypic *Labiostrombus* (*Labiostrombus epidromis* (Linnaeus, 1758)) were selected as outgroups based on the DNA sequence based phylogeny contained in Latiolais *et al.* (2006), these also share a general structural form and spatiotemporal similarity and were included to test their relationship with the focus genera, *Dolomena* (Abbott 1960; Kronenberg 1998; Maxwell *et al.* 2019a, b).

All species attributed to *Dolomena* Wenz, 1940 ex Abbott (1960) and its subsequent taxonomic

derivatives were considered, the types for the outgroups were examined, and twenty-three characteristics were coded based on this examination (Table 1). We focus on three regions of the shell for character coding. The first region included the aperture and columella, which fall into three subcategories (see Table 1) namely: the outer lip including the labellum and shape of the stromboidal lobe (Characteristics 1-4, and 12; Figure 1); the shape of the columella (Characteristics 5-7; Figure 1); and the shape of the posterior sinus (Characteristics 8-11; Figure 1). The second region dealt with the shape of the ventral body whorl (Characteristics 13-17; Figure 1). The third set of characters was drawn from the dorsal body whorl (Characteristics 18-21; Figure 1) and the dorsal spire (Characteristics 22-23; Figure 1). We used MEGA X (Kumar *et al.* 2018) to analyse morphological characters inferring the maximum parsimony phylogeny using a Max-branch and bound method. The generation of the phylogeny occurred in two phases. The first, at the rank of genera using the type species. When the outgroups *Doxander* Wenz, 1940 and *Labiostrombus* Oostingh, 1925 were found to be nested within the *Dolomenini tribus nov.*, all species contained within those nested taxa were included in the second round of analysis. This process avoided the algorithm inferring homologies at the rank of genera leading to distortion in the internal resolution of the phylogeny. The stability of all trees generated was undertaken using 500 bootstrap replications. Synapomorphies were then examined in terms of the fossil record and the phylogeny generated. We then demarcated relationships based on the phylogeny and defined them under the guidelines of the PhyloCode (2014). Where identified clades from the character analysis reflected the historical generic affiliation, the existing taxonomy was retained. Material examined to determine character sets were incorporated within the assigned taxa lists.

SYSTEMATICS

Dolomenini tribus nov. was found to contain two distinct subclades (Figure 2A): the first, *Doxanderina subtribus nov.* contained monophyletic *Doxander* and *Neodilatilabrum* Figure 2B; and the second *Dolomenini tribus nov.*, contained monophyletic *Dolomena*, *Labiostrombus*, *Amabiliplicatus gen. nov.*, *Pacificus gen. nov.* and *Dominus gen. nov.* and *Ministrombus* (Figure 2C). The clustering of *Neodilatilabrum* and *Doxander* within *Doxanderina subtribus nov.*, and the nesting of *Labiostrombus* within the *Dolomenini tribus nov.* are major revisions in Stromboid systematics.

Phylum	Mollusca Linnaeus, 1758
Superorder	Caenogastropoda Cox 1960
Order	Sorbeoconcha Ponder & Lindberg, 1987
Superfamily	Stromboidea Rafinesque, 1815
Epifamily	Neostromboidae Maxwell, Dekkers, Rymer & Congdon, 2019
Family	Strombidae Rafinesque, 1815

Dolomenini tribus nov.

Type Genus. *Dolomena* Wenz, 1940, p. 945.

Definition. The clade has the characteristics outlined in the diagnosis, and contains *Dolomena* Wenz, 1940, *Doxander* Wenz, 1940, *Labiostrombus* Oostingh, 1925 and *Neodilatilabrum* Dekkers, 2008 and taxa more closely related to them than to other members of Strombidae Rafinesque, 1815.

Diagnosis. Early to mid-teleoconch with even axial ornamentation. Outer lip without ornamentation, anterior canal short, shoulder of body whorls with knobs that may be greatly reduced.

Etymology. Based on the genus group name *Dolomena* Wenz, 1940.

Doxanderina subtribus nov.

(Figure 3)

Type Genus. *Doxander* Wenz, 1940, p. 945.**Definition.** The clade has the characteristics outlined in the diagnosis, and contains *Doxander* and taxa more closely related to it than members of the Dolomenina new subtribe.**Diagnosis.** The aperture of the shell is uniformly lirate. There is no marginal fold present on the edge of the outer lip. The outer lip lacks sharpness. The body of the shell is rounded, with a convex flange that may be stepped. There is no flange fold. The spire is sculptured with uniform axial ribs. The columella is straight and mostly smooth. The posterior sinus has uneven sides with the outer side being sharp-edged.**Etymology.** The name is based on the genus group name *Doxander* Wenz, 1940.***Doxander* Wenz, 1940**

(Figures 3A-E)

Type Species. *Strombus vittatus* Linnaeus, 1758, p. 545, no. 439 (Wenz, 1940, p. 945).**Definition.** The clade has the characteristics outlined in the diagnosis, and contains all recent members of the *Doxanderina subtribus nov.* not included within *Neodilatilabrum* Dekkers, 2008.**Original Description.** "Gehäuse groß bis sehr groß, schlank, spindelförmig; Gewinde hoch; Umgänge gewölbt, mit schmalem, glattem Streifen unter der Naht und axialen Rippen; Endwindung fast glatt oder mit mehr oder weniger deutlichen axialen Rippen, auf der unteren Hälfte mit Spiralrillen" (Wenz 1940, p. 945). [Translation: Shell large to very large, slender, spindle-shaped; high spire; whorls rounded, with small spiral lines under the suture and axial ribs; body whorl almost smooth or with distinct axial ribs on the lower half with spiral grooves].**Diagnosis.** Shells with a high spire. The body whorl is smooth or with strong axial folds or spiral lines. The dorsum is often with a central knob on the shoulder. The subsutural cord is well defined. The inside labrum has weak or stronger lirae. Stromboidal notch moderately well formed. The flange is stepped.**Synonymy.** Not *Doxander* Iredale (1931, p. 212): the changing of the ICZN (1985; 1999 Article 13.1) made the name unavailable as Iredale (1931) gave only a name without description. Thus, the name remained a *nomen nudum* until redescribed by Wenz (1940).**Assigned Taxa:***Strombus (Doxander) vittatus apicatus* Man in 't Veld and Visser, 1993, p. 19, pl. 2, figs. 1-6 [= *Strombus (Doxander) vittatus vittatus* form *australis* Schröter, 1805 ex Abbott (1960, p. 113)]. Type Locality: Brunei, Borneo, Kuala Belait (Man in 't Veld and Visser 1993) (Figure 3A). Material examined. THAILAND - Trawled Gulf of Thailand (SMC x 6), Bun Hua Him, Gulf of Thailand (AMD x 1), off Phuket Island (AMD x 1); VIETNAM - off Nha Trang (AMD x 1; SMC x 3).*Strombus campbelli* "Gray" Griffith and Pidgeon, 1834, p. 600, pl. 25, fig. 6 [= *Strombus (Doxander) vittatus campbelli* Griffith and Pidgeon, 1834 ex Abbott (1960, p. 113, pl. 17, fig. 18)]. Type Locality: Bowen, Queensland (Abbott 1960) (Figure 3B). Material examined: AUSTRALIA - Yirrkala, Gove, Northern Territory (SMC x 1), Amity Point, Stradbroke Island, Queensland (SMC x 2), Bountiful Island, Gulf of Carpentaria, Queensland (SMC x 1), Alexandra Reef, Queensland (SMC x 1), Cape York Peninsula, Queensland (SMC x 2), Dalrymple Point, Bowen, Queensland (SMC x 1), Dingo Beach, Queensland (AMD x 5; SMC x 91), Fraser Island, Queensland (SMC x 6), Gloucester Passage, Queensland (AMD x 2; SMC x 5),

Horseshoe Bay, Magnetic Island, Queensland (SMC x 3), King Reef, Queensland (SMC x 3), Kurrimine Beach, Queensland (AMD x 1; SMC x 6), Pallaranda, Queensland (SMC x 1), Pancake Creek, Queensland (SMC x 1), S.E. Mooloolaba, Queensland (SMC x 1), Saunders Beach, Queensland (SMC x 9), Shellbourne Bay, Queensland (SMC x 1), Shelly Beach, Townsville, Queensland (SMC x 14), Shoal Point, Mackay, Queensland (AMD x 2; SMC x 2), Thursday Islands, Torres Straits, Queensland (SMC x 1), Trawled off Townsville, Queensland (SMC x 19), Wonga Beach, Queensland (SMC x 2), Cape Kerau Dren, Western Australia (SMC x 1), Dampier Archipelago, Western Australia (AMD x 1), Jarman Island, Wickham, Western Australia (SMC x 3), Port Headland, Western Australia (AMD x 3; SMC x 2), Reginald Bay, Western Australia (SMC x 1), Rowley Shoals, Western Australia (SMC x 1), Shark Bay, Western Australia (AMD x 1; SMC x 2), Town Beach, Broome, Western Australia (SMC x 6).

Strombus (Doxander) vittatus entropi Man in't Veld and Visser, 1993, p. 26, pl. 2, figs. 7–12 [= *Strombus (Doxander) vittatus vittatus* Linnaeus, 1758 fide Abbott (1960, p. 111, pl. 17, fig. 14)]. Type Locality: Cañacao Bay, Sangley Point, Manila Bay, Luzon Island (after the holotype locality- Man in't Veld and Visser 1993). Material examined: MALAYSIA - Kudat, Sabah (AMD x 1); PHILIPPINES - Aliguat Island (SMC x 1), Bohol (AMD x 2), Matuban Island (AMD x 1), Masbate (AMD x 2), Calituban Island (SMC x 4), Davao (SMC x 21).

Strombus japonicus Reeve 1851, pl. 17 [= *Strombus (Doxander) vittatus japonicus* Reeve, 1851 fide Abbott (1960, p. 113, pl. 17, fig. 18)]. Type Locality: Nagasaki, Japan (Abbott 1960) (Figure 3D). Material

examined: JAPAN - Chiba (SMC x 1), Mikawa Archi prefecture (AMD x 1), Kii Straits (AMD x 3), Tosa Bay (AMD x 3).

Strombus vittatus Linnaeus, 1758, p. 545, no. 439 [= *Strombus (Doxander) vittatus vittatus* Linnaeus, 1758 ex Abbott (1960, p. 111)]. Type Locality: Ambon, Indonesia (Abbott 1960) (Figure 3E). Material examined: AUSTRALIA - Bountiful Island, Gulf of Carpentaria, Queensland (SMC x 2), Buchans Beach, Queensland (SMC x 1), Cape York Peninsula, Queensland (SMC x 1), Cook Reef, Torres Straits, Queensland (SMC x 1), Dingo Beach, Queensland (SMC x 19), Four Mile Beach, Port Douglas, Queensland (SMC x 2), Off Gladstone, Queensland (AMD x 3), Hinchinbrook Island, Queensland (AMD x 1), Keppel Bay, Queensland (SMC x 1), Kurrimine Beach, Queensland (SMC x 2), Moreton bay, Queensland (AMD x 1), Palm Island, Queensland (SMC x 1), Saunders Beach, Queensland (SMC x 2), Shelly Beach, Townsville, Queensland (SMC x 2), Shoal Point, Mackay, Queensland (SMC x 2), Stradbroke Island, Queensland (AMD x 1), Trawled off Townsville, Queensland (SMC x 3).

***Neodilatilabrum* Dekkers, 2008**

(Figures 3F-K)

Type Species. *Strombus marginatus* Linnaeus, 1758, p. 744, no. 431 (Dekkers, 2008).

Definition: The clade has the characteristics outlined in the diagnosis, and contains all recent members of the *Doxanderina* nov. subtribus not included within *Doxander* Wenz, 1940.

Original Description. “Shell small to medium sized, solid shells. Form of shell elongated. Spire medium to tall, body whorl not much decorated; the shoulder with a keel or evolved to a more round shoulder. Columella and aperture smooth, but inside of the not much

flaring lip decorated with little knobs. A stromboid notch is present” (Dekkers 2008, p. 58).

Diagnosis. Stromboidal notch sinuous. The flange is not stepped. Spire with distinct shoulder with knobs. Body whorl shiny and almost without any sculpture; expanded outer lip thickened at the inner edge and smooth. Aperture smooth within. Columellar smooth, with callous, well-marked. The anterior canal is short. The stromboid notch is moderately developed. The posterior canal is present.

Synonymy. *Margistrombus* Bandel, 2007, p. 153 is not accepted as valid under ICZN (1999) Article 13.1.1: “To be available, every new name published after 1930 must satisfy the provisions of Article 11 and must be accompanied by description or definition that states in words characters that are purported to differentiate the taxon”. However, Bandel (2007) described the selected type species. That is not fulfilling the strict requirements of Article 13 and therefore his proposed generic names are unavailable.

Assigned taxa:

Strombus marginatus Linnaeus, 1758, p. 744, no. 430 [= *Strombus (Dolomena) marginatus marginatus* Linnaeus, 1758 ex Abbott (1960, p. 98, pl. 18, figs. 6, 7)]. Type Locality: Sri Lanka (Abbott 1960) (Figure 3G). Material examined: INDIA - (SMC x 1), Cuddalore (AMD x 1), Deuipatnam (SMC x 1), Gulf of Bengal (AMD x 2), Kilakari (SMC x 1), Kilarkarai (SMC x 1), (AMD x 2), Kottai Pattanam (AMD x 8), Off Madras (AMD x 1; SMC x 1), Rameswarum (AMD x 1), Off Tondi (AMD x 1); SRI LANKA - Galle (AMD x 1), Trincomalee (AMD x 1; SMC x 2).

Strombus robustus Sowerby, 1875, p. 599, pl. 72, figs. 5, 5a. Type Locality: Hong Kong (Abbott, 1960) (Figure 3F). Synonym: *Margistrombus boucheti* Thach, 2016, pp. 39 – 40, fig. 2. Type Locality: Nha Trang

area, Khan Hoa Province, Vietnam (Thach 2016) (Figure 3F). Material examined: JAPAN - Bay of Tanabe (AMD x 1); SINGAPORE - Changi Coast Road (AMD x 1).

Strombus septimus Duclos, 1844, p. 7, pl. 13, figs. 9, 10 [= *Strombus (Dolomena) marginatus septimus* Duclos, 1844 ex Abbott (1960, p. 101, pl. 18, figs. 10, 11)]. Type Locality: Lusong, Luzon Island, Philippines (Abbott 1960) (Figure 3I). Material examined: MICRONESIA - Anguar, Palau (AMD x 1); PAPUA NEW GUINEA - (SMC x 3), Rabaul (AMD x 1); PHILIPPINES - Balicasag Island (SMC x 1), Bohol (AMD x 3), Garidad, Panay (AMD x 1), Luxon Island (AMD x 1), Manila Bay (AMD x 1), Negros Islands (AMD x 6); SOLOMON ISLANDS - Marapa Island (AMD x 1), Marau Sound (AMD x 2), Guadalcanal (AMD x 1); TAIWAN - Off Anping (AMD x 1); VANUATU - Vanuatu (AMD x 1).

Margistrombus simanoki Liverani, 2013, p. 77, pl. 1, figs. 1, 2. Type Locality: Tapaktuan, Aceh Province, northern end of Sumatra Island, Indonesia (Liverani 2013) (Figure 3J). Material examined: The photos from original publication: none in collections.

Strombus (Dolomena) marginatus sowerbyorum Visser & Man in't Veld, 2005, p. 58, Pl. 1. figs. 3,4; pl. 2, fig. 2; pl. 3, figs. 3, 4. [= *Strombus (Dolomena) marginatus robustus* Sowerby, 1874 (sic = 1875) ex Abbott (1960, p. 100, pl. 18, figs. 13, 14)]. Type Locality: Borneo, Brunei, Kuala Belait. ex coll. J.N.J. Post (Visser & Man in't Veld, 2005) (Figure 3H). Material examined: INDONESIA - (SMC x 1); TAIWAN: (SMC x 1); THAILAND - East Coast (SMC x 2); PHILIPPINES - Cebu Island (SMC x 1), Corregidor Island (SMC x 1); JAPAN – Kominato Chib (SMC x 4), Okinawa (SMC

x 4); VIETNAM - An Dang Beach (AMD x 2), Mui Ne (AMD x 1).

Strombus succinctus Linnaeus, 1767, p. 1212, no. 509 [= *Strombus (Dolomena) marginatus succinctus* Linnaeus, 1767 ex Abbott (1960, p. 99, pl. 18, figs. 13, 14)]. Type Locality: Madras, India (Abbott 1960) (Figure 3J). Material examined: INDIA - (AMD x 1), Cuddalore (AMD x 1), Kottai Pattinam (AMD x 5), Madras (AMD x 13; SMC x 5), Tuticorin (AMD x 2); SRI LANKA - Galle (AMD x 1), Lavinia (AMD x 1).

Dolomenina subtribus nov.

(Figure 4)

Type Genus. *Dolomena* Wenz, 1940, p. 945.

Definition: The clade has the characteristics outlined in the diagnosis, and contains *Dolomena* Wenz, 1940, and all taxa more closely related to it than members of *Doxander* Wenz, 1940, and *Neodilatilabrum* Dekkers, 2008.

Diagnosis. Shell with uniform spiral sculpture of fine axial ribs. The flange is convex, and a flange fold runs from the posterior end of the labrum to the anterior end, mostly following the outline of the outer edge of the labrum, and only becoming obsolete at both ends.

Etymology. Based on the genus group name *Dolomena* Wenz, 1940.

***Dolomena* Wenz, 1940**

(Figures 4A-C)

Type Species. *Strombus pulchellus* Reeve, 1851, fig. 52.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Strombus pulchellus* Reeve, 1851, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus nov.*

Original Description. "Gehäuse mittelgroß, breiter; Außenrand der Mündung besonders oben mehr ausgebreitet; Endwindung mit einer weiteren, tieferstehenden Reihe kleiner Höcker" (Wenz 1940, p. 945) [Translation: Shells of medium size, broader; outer lip especially broader at the posterior end; body whorl with a second lower row of small knobs].

Diagnosis. Shells from 2 cm to 6 cm. Spire with distinct shoulder and with knobs mostly axially aligned. Body whorl with small knobs dorsally and spiral ribbing that can become obsolete. A hardly noticeable second row of very small knobs is present at the mid-whorl, where the outline of the shell has a nick. Expanded outer lip broader at the posterior end and flattened toward the rim. Aperture lirate within, stained with brown colour entering the aperture. Columellar callous present but small on the ventral side, marked, with lirae at the upper half, which are white or brown coloured. A brown background colour is often found deeper within the aperture. Lower half of the columella smooth and with thickened callous. Anterior canal short but always longer than the anterior part of the outer lip. Deeply incised stromboid notch.

Synonymy. *Dolomena* Wenz, 1940, p. 945 [Not *Dolomena* Iredale (1931, p. 212): the changing rules of the ICZN (1999) made the name unavailable as Iredale (1931) gave only a name without description. Thus, the name remained a *nomen nudum* until the first description was provided by Wenz (1940)].

Assigned Taxa:

Strombus columba Lamarck, 1822, p. 208 [= *Strombus (Dolomena) plicatus* subspecies *columba* Lamarck, 1822 ex Abbott (1960, p. 90, pl. 18, figs. 1, 2)]. Type locality: Zanzibar (Abbott 1960) (Figure 4A). Material examined: MOZAMBIQUE - Nacala Bay (AMD x 5; SMC x 1); SEYCHELLES - Mahe (AMD x 1), Off

Victoria, Mahe (AMD x 2); TANZANIA - (AMD x 1); Nungi, Zanzibar (AMD x 1).

Strombus (Labiostrombus) hickeyi Willan, 2000, p. 20, pl.1, figs. 1, 2. Type locality: Bowen, Queensland (Willan 2000) (Figure 4B). Material examined: AUSTRALIA - Bowen Sand Flats, Queensland (SMC x 1), Dingo Beach, Queensland (AMD x 4; SMC x 9), Green Island, Queensland (SMC x 1), Palm Island, Queensland (AMD x 1; SMC x 2), Shellbourne Bay, Queensland (SMC x 1).

Strombus pulchellus Reeve, 1851, fig. 52 [= *Strombus (Dolomena) plicatus* subspecies *pulchellus* Reeve, 1851 ex Abbott (1960, p. 92, pl. 63, fig. 2)]. Type Locality: Philippines (Abbott 1960) (Figure 4C). Material examined: AUSTRALIA - Dingo Beach, Queensland (SMC x 1), East of Noosa, Queensland (SMC x 2), Dampier, Western Australia (SMC x 1); CHINA - South of Palau Subi Besar (AMD x 2); INDIA - Off Chennai (AMD x 2), Off Ervadi SE Coast (AMD x 1), Tuticorin (AMD x 2); INDONESIA - Wasir Island (SMC x 1); NEW CALEDONIA - Gue Reef (AMD x 10); PAPUA NEW GUINEA - Rabaul (AMD x 2; SMC x 1), Samuray (AMD x 1); PHILIPPINES - Aliquay (AMD x 5), Balicasag Island (AMD x 2), Balut Island (AMD x 1), Birat and Kanipaan, Samal (AMD x 2), Bogo (SMC x 1), Bohol (AMD x 2), Calituban Island (AMD x 1), Cardidad, Panay (AMD x 1), Cebu Island (AMD x 1; SMC x 1), Davau Island (SMC x 1), Mactan (AMD x 1), Olango (AMD x 6), Palawan (AMD x 1), Samar (AMD x 1), Santa Rosa Island, Cebu (AMD x 1), Tinina Balut Island (SMC x 1); MALAYSIA - Kudat, Sabah (AMD x 1); MICRONESIA - Orote Point, Guam (AMD x 2); SOLOMON ISLANDS - Bonegi (SMC x 1), Honiara (SMC x 1), Kakabona, Guadalcanal (SMC x 1), Makina Passage (AMD x 2), Marau

Sound (AMD x 16); THAILAND - Port Dickson (AMD x 1).

***Labiostrombus* Oostingh, 1925** (Figure 4D)

Type Species. *Strombus epidromis* Linnaeus, 1758, p. 745, no. 436.

Definition. The characteristics outlined in the diagnosis, and contains *Strombus epidromis* Linnaeus, 1758, and all taxa more closely related to it than the defining members of any other clade within Dolomenina new sub tribe.

Original Description: "Genus XIII Gallinula § 164 Gallinis incubantibus adsimilamus Volutas gibbas acute muronatas; labia expanso instar alae; in acumen terminatas" (Klein 1753, p. 56). [Translation: as like a brooding chicken (sic) not unlike *Voluta gibbas* with a distinct point; flange expanded and wing like; terminating in a sharp point]. Oostingh (1925, p. 58) defined *Strombus (Labiostrombus)* as the replacement name for *Gallinula* "Kl" Mörch, 1852, p. 61 and gave attribution to "(Klein) Herrmannsen, 1847, H. & A. Adams, 1854" [non Brisson, 1760 - Aves].

Diagnosis. Shell with smooth aperture and columella. The outer lip has a marginal fold and is uniformly calloused towards the edge. The columella is straight. The dorsum has low small knobs or ribs. Spire uniformly sculptured with axial ribs.

Synonymy. *Gallinula* "Klein" Mörch 1852, p. 61.

Assigned Taxa:

Strombus epidromis Linnaeus, 1758, p. 745, no. 436 [= *Strombus (Labiostrombus) epidromis* Linnaeus, 1758 ex Abbott (1960, p. 107, pl. 83, figs. 1, 2)]. Type Locality: Amboina, Indonesia (Abbott 1960) (Figure 4D). Material examined: AUSTRALIA - Trawled off Townsville, Queensland (SMC x 1), Broome, Western Australia (SMC x 1), Swains Reef (AMD x 1); INDONESIA -

Bengkulu, West Sumatra (AMD x 1), Pendangaran (AMD x 1); MALAYSIA - Sikuati, Sabah (AMD x 1); NEW CALEDONIA - Boats Pass (AMD x 2), Goeland Island (SMC x 1), Grande Goude (AMD x 1), Noumea (SMC x 1), Poum (AMD x 1), Thio (AMD x 6); CHINA - South China Sea (AMD x 1), THAILAND - Gulf of Thailand (SMC x 2); PAPUA NEW GUINEA - Kokopo (SMC x 2), Rabaul (AMD x 2), Tubesseria (AMD x 1); PHILIPPINES - Batayan Island (AMD x 1), Bohol (AMD x 2), Calituban Island (AMD x 1), Cebu (AMD x 1), Dumanhug (AMD x 2), Off Maya, Cebu (AMD x 1), Olango (AMD x 2), Placer, Masbate (AMD x 1), Siasi, Sulu Sea (AMD x 1); VANUATU - Vanuatu (AMD x 1).

***Ministrombus* Dekkers, 2010**

(Figures 4E-G)

Type Species. *Strombus minimus* Linnaeus, 1771, p. 549.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Strombus minimus* Linnaeus, 1771, and all taxa more closely related to it than the defining members of any other clade within *Supradolomina subtribus nov.*

Original Description. Shell “with pointed spire (40 degrees) with a median corner that bears nodes. The outer lip forms a lobe on a ridged end and is attached to the suture or above the body whorl. A thickened callus ridge of inner lip continuous to the posterior canal. The siphonal canal is wide and upturned. Shell size ranges from 20-65 mm” (Dekkers 2010, p. 9).

Diagnosis. The spire has a distinct shoulder with knobs. The body whorl is shiny and almost without any sculpture. The expanded outer lip is thickened at the inner edge and is shiny and smooth. The aperture is smooth within. The columellar is smooth, with a well-defined

callous. The anterior canal is short. The stromboid notch is medium deep. The posterior canal is present.

Synonymy. *Ministrombus* Bandel, 2007, p. 154, is not accepted as valid under ICZN (1999) Article 13.1 [see *Margistrombus* Bandel, 2007 above].

Assigned Taxa:

Strombus athenius Duclos, 1844, p. 7, pl. 11, fig. 2 [= *Strombus (Dolomena) variabilis athenius* Duclos, 1844 ex Abbott (1960, p. 104, pl. 79, figs. 3, 4)]. Type Locality: Biak Island, Dutch New Guinea (= Indonesia, Abbott 1960) (Figure 5E). Material examined: AUSTRALIA - Green Island, Queensland (SMC x 1); PAPUA NEW GUINEA - New Britain (SMC x 2), Milne Bay (SMC x 4); NEW CALEDONIA - (SMC x 2), Arama (SMC x 1), Plage de Baffade (SMC x 3).

Strombus minimus Linnaeus, 1771, p. 549 [= *Strombus (Dolomena) minimus* Linnaeus, 1771 ex Abbott (1960, p. 105, pl. 18, figs. 2, 5)]. Type Locality: Cebu City, Philippines (Abbott 1960) (Figure 5F). Material examined: AUSTRALIA - James' Point, WA (AMD x 1); INDONESIA - Waiara, Flores (AMD x 4); NEW CALEDONIA - Beleps Islands (AMD x 1); NEW HEBRIDES - Vila (AMD x 3); PAPUA NEW GUINEA - Kokopo (SMC x 5), Port Moresby (SMC x 2); Rabaul (SMC x 5); PHILIPPINES - Bantagas (AMD x 1), Bohol (AMD x 1), Balabac Island (AMD x 1), Balicasag Island (SMC x 1), Batangas (AMD x 5), Bohol (AMD x 6), Palawan (AMD x 1), Punta Engano, Cebu (AMD x 1), Quezon (AMD x 1), Zamboanga (AMD x 1); SOLOMON ISLANDS - Ghizo Harbour (SMC x 1), Guadalcanal (AMD x 4; SMC x 1), Ngella Island (SMC x 2); VANUATU - (AMD x 4; SMC x 1).

Strombus variabilis Swainson, 1820, pl. 10 [= *Strombus (Dolomena) variabilis* subspecies

variabilis Swainson, 1820 ex Abbott (1960, p. 103, pl. 79, figs. 1, 2)]. Type Locality: Cebu, Philippines (Abbott 1960) (Figure 5G). Material examined: AUSTRALIA - Fairy Reef (AMD x 1), Swains Reef (AMD x 2); INDONESIA - Off Batu Belubang, NE Bangka Island (SMC x 1); JAPAN - East China Sea (AMD x 1); MALAYSIA - Gaya Island, Sabah (AMD x 2), Kota Kinabalu, Borneo (AMD x 3), Kudat, Sabah (AMD x 1), Miri, Sarawak (AMD x 1); MARSHAL ISLANDS - Kwajalein (SMC x 6); PAPUA NEW GUINEA - Rabaul (AMD x 2); PHILIPPINES - Aliguay Island (SMC x 1), Balabac, Palawan (AMD x 2), Bohol (AMD x 1), Calituban Island (AMD x 1), Caubian Deep (AMD x 1), Cebu (AMD x 6), Dinagat Island, Surigao (SMC x 3), Don Island (SMC x 4), Maasin, Leyte (AMD x 1), Masbate (AMD x 6), Maya, Cebu (AMD x 2), Nocnocan Island (AMD x 1), Olango (AMD x 4), Pagbilao Bay (AMD x 4), Pandagang island (AMD x 1), Palawan (AMD x 2), Polilio Island (AMD x 4), Samar (AMD x 3), Sulu (AMD x 4), Talicud Island, Samal (AMD x 1); THAILAND - Bangirak (AMD x 1), Koh Mak (AMD x 7), Off Phuket (AMD x 2); TAIWAN - (AMD x 2); TONGA - Vavua Islands (AMD x 1).

***Amabiliplicatus* gen. nov.**

(Figures 4H-J)

Type Species. *Lambis plicata* Röding, 1798, p. 65, no. 835.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Lambis plicata* Röding, 1798, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus* nov.

Diagnosis. The spire rather high with shallow knobs and infrequent old varices. The body whorl is broad, with spiral ribbing that becomes coarser towards the anterior end, with small

knobs rounded or stretched axially on the rounded shoulder. The shell has a broadly expanded outer lip. The aperture is coarsely lirated within, white or stained with brown. The columellar callous is present but small. The columella is fully lirated, often brown coloured on the lirae. The anterior canal is very short but broad. Strombus notch broad but shallow.

Etymology. The name is a combination of the Latin words *amibilis* meaning “lovely” and *plicatus* meaning “plicate” for the axially stretched ribbing on the dorsum of species belonging to this genus.

Assigned Taxa:

Lambis plicata Röding, 1798, p. 65, no. 835 [= *Strombus (Dolomena) plicatus plicatus* (Röding, 1798) ex Abbott (1960, p. 89, pl. 18, fig. 12)]. Type locality: Red Sea (Abbott 1960) (Figure 4H). Material examined: EGYPT - Abu Mad (AMD x 2), Hurghada (AMD x 1), Marsa Sleemet (SMC x 2), Ras Zafarana (AMD x 1).

Strombus sibbaldi Sowerby, 1842, p. 28, pl. 6, figs. 10, 11 [= *Strombus (Dolomena) plicatus sibbaldi* Sowerby, 1842 ex Abbott (1960, p. 91, pl. 18, fig. 15, 16)]. Type locality: Ceylon (= Sri Lanka, Sowerby 1842) (Figure 4I). Material examined: INDIA - Off Madras (AMD x 1), Kollam, Kerala (AMD x 3; SMC x 2), Rameswaram (AMD x 1), South East Coast (AMD x 1; SMC x 1), West Coast (SMC x 1).

Strombus yerburyi Smith, 1891, p. 419, pl. 33, fig. 5 [= *Strombus (Dolomena) plicatus sibbaldi* Sowerby, 1842 ex Abbott (1960, p. 92)]. Type locality: Gulf of Aden, Arabian Sea (Smith 1891) (Figure 4J). Material examined: DJIBOUTI - (AMD x 1); SOMALIA - (SMC x 3), Off Cape Guardafui, Suqutra Island (AMD x 1), Ras Hafun (AMD x 1), South of Mogadishu (AMD x 1), North Coast (AMD x 1); YEMEN - Aden (AMD x 1).

Dominus gen. nov.

(Figures 5A-C)

Type Species. *Strombus labiosus* Wood, 1828, p. 54, pl. 4, fig. 3.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Dolomena wieniekei* Wiersma & Monsecour, 2012, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus nov.*

Diagnosis. The spire with a distinct shoulder and knobs mostly axially aligned. The body whorl has medium knobs dorsally on the shoulder, and weak spiral ribs. The expanded outer lip has a strongly thickened end. The posterior outer lip is horizontal or pointing slightly upwards to the posterior. The aperture is lirate within. The columellar callous is mostly smooth or weakly lirate. The anterior canal is rather short.

Etymology. The name is derived from the Latin *dominus*, meaning “lord”.

Assigned taxa:

Dolomena abbotti Dekkers & Liverani, 2011, p. 111, pl. 1, fig. 6 and pl. 2, figs. 10-12 [= *Strombus (Dolomena) labiosus* Wood, 1828 ex Abbott (1960, p. 95, pl. 18, figs. 17-19)]. Type Locality: Phuket, Andaman Sea (Dekkers and Liverani 2011) (Figure 5A). Material examined: THAILAND - Kantang (AMD x 1), Korbon Island (AMD x 1), Ranong (AMD x 1), Rawai, Phuket (AMD x 1); INDONESIA - Off Sarni, Irian Jaya (AMD x 1), Off Racha Island, Andaman Sea (SMC x 1); MALAYSIA - Kota Kinabalu, Borneo (AMD x 1), Sedili, Johor (AMD x 2); PHILIPPINES - Bohol Island (SMC x 1), Cebu Island (SMC x 1); SINGAPORE - (AMD x 3).

Dolomena wieniekei Wiersma & Monsecour, 2012a, p. 37 [= *Strombus (Dolomena) labiosus* Wood, 1828 ex Abbott (1960, p. 95, pl. 69, figs. 1, 2)]. See Wiersma &

Monsecour (2012b) for an amended description. Type Locality: Northern Coast of New Britain, Kimbe Plantation, Papua New Guinea (Wiersma & Monsecour 2012a) (Figure 5B). Material examined: PAPUA NEW GUINEA - Off Goodenough Island (AMD x 3), Rabaul (SMC x 3).

Strombus labiosus Wood, 1828, p. 54, pl. 4, fig. 3 [= *Strombus (Dolomena) labiosus* Wood, 1828 ex Abbott (1960, p. 95)]. Type Locality: Tuléar, west Madagascar (Dekkers & Liverani 2011) (Figure 5C). Material examined: MADAGASCAR - Tulear (AMD x 9; SMC x 1); MOZAMBIQUE - Pamba Island (AMD x 3), Seven Tree Island (AMD x 1); SRI LANKA - (AMD x 1).

Pacificus gen. nov.

(Figures 5D-F)

Type Specie. *Strombus dilatatus* Swainson, 1821, pl. 71.

Definition. This clade has the characteristics outlined in the diagnosis, and contains *Strombus dilatatus* Swainson, 1821, and all taxa more closely related to it than the defining members of any other clade within *Dolomenina subtribus nov.*

Diagnosis. The spire has a distinct (angular) shoulder with knobs axially aligned and spiral ribbing, old varices present. The body whorl has small knobs dorsally and faint spiral ribbing. The outer lip is expanded and flattened towards the edge. The inner lip is calloused at the edge. The aperture is lirate within. The posterior canal is present and bends towards the spire. The columellar callous is well formed, and lirate posteriorly and never coloured. The anterior canal is rather short but broad. Stromboid notch is broad and shallow.

Etymology. The name is derived from the Latin word *pacificus* meaning “peaceful”.

Assigned Taxa:

Strombus dilatatus Swainson, 1821, pl. 71 [= *Strombus (Dolomena) dilatatus dilatatus* Swainson, 1821 ex Abbott (1960, p. 93, pl. 66, fig. 2)]. Type Locality: Upala Cay (= Upolo Cay), Queensland, Australia (Abbott 1960) (Figure 5D). Material examined: AUSTRALIA - Bowen, Queensland (SMC x 3), Cape Morten, Queensland (SMC x 6), Dingo Beach, Queensland (AMD x 5; SMC x 16), East of Noosa, Queensland (SMC x 55), Gould Reef, Queensland (SMC x 2), Green Island, Queensland (SMC x 1), Keppel Bay, Queensland (AMD x 2; SMC x 1), North West Is. Capricorn Group, Queensland (SMC x 1), Off Sandy Cape, Queensland (AMD x 1; SMC x 2), Palm Island, Queensland (SMC x 8), Swains Reefs, Queensland (AMD x 3; SMC x 1), Townsville, Queensland (AMD x 2; SMC x 6), Trunk Reef, Queensland (SMC x 4); NEW CALEDONIA - Armama (SMC x 1); SOLOMON ISLANDS - (SMC x 1).

Strombus orosminus Duclos, 1844, p. 6, pl. 10, figs. 10, 11 [= *Strombus (Dolomena) dilatatus dilatatus* form *orosminus* Swainson, 1821 ex Abbott (1960, p. 93, pl. 66, fig. 2)]. Type Locality: Duclos, 1844 gave no type locality, nor did Abbott (1960); we hereby designate Olango Island, Philippines (Figure 5E). Material examined: PHILIPPINES - Davau Island (SMC x 1), Olango (AMD x 2), Mactan (AMD x 2).

Strombus swainsoni Reeve, 1850, figs. 28a, [= *Strombus (Dolomena) dilatatus swainsoni* Reeve, 1850 ex Abbott (1960, p. 94, pl. 66, fig. 1)]. Type Locality: Reeve, 1850 gave no locality, nor did Abbott (1960); we hereby designate Nha Trang, Khánh Hòa Province, Vietnam (Figure 5F). Material examined: VIETNAM - Danang (SMC x 1), Off Nha Trang (AMD x 10; SMC x 2); CHINA - South China Sea (AMD x 7).

DISCUSSION

The clade *Dolomenini tribus nov.* divides into two, *Dolomenina subtribus nov.* and *Doxanderina subtribus nov.*, whose characteristics are well established in the Pliocene and perhaps late Miocene. *Neodilatilabrum rutteni* (Altena, 1942) from the Pliocene of Java and *Pacificus togopiensis* (Cox, 1948) from the Pliocene of Java, are early members of *Doxandrina subtribus nov.*, both having straight and smooth columellas, a stepped in-curved flange and interior lirations typical of that clade. *Neodilatilabrum rutteni* is a fossil species with a sharp outer lip, triangulate shoulder, interior liration, and even its sculpture is not dissimilar to members of *Neodilatilabrum*, but it lacks the curved flange of *Doxanderina subtribus nov.* The recognition of *Dolomenina subtribus nov.* reflects its long fossil record in the Indo-Pacific. *Dominus fennemai* (Martin, 1899) and *Dominus teschi* (Cox, 1948) from the Pliocene of Indonesia show the straight flange with a folded, sinuous columella, and cuneate dorsal body whorl.

The recently described *Doxander bruneiensis* (Harzhauser *et al.*, 2018; Late Miocene, Borneo) is reassigned from *Dolomena* based on the subsutural cord, the simple outer lip and the strong lirae inside the labrum that is a characteristic diagnostic of the genus *Doxander*. It is most likely an early representative of that genus with a more compact shell; a form that evolved into the extant species that have a more elongated spire, with the diagnostic characters remaining unchanged.

The fossil *Labiostrombus denti* Cox, 1948 (Pliocene, Java) indicates that *Labiostrombus* has a long fossil record at least from the Miocene to the present day. Willan (2000) synonymized *Dolomena* with *Labiostrombus* Oostingh, 1925, and this debatable taxonomic

arrangement was not followed by subsequent authors (Bandel 2007; Dekkers 2008; Liverani 2013). Notwithstanding, we found that *Labiostrombus* was not nested with the wider *Dolomena* complex.

CONCLUSION

The beauty of phylogenetic nomenclature is that these definitions can be redefined as our understanding of the internal structure improves. Notwithstanding future shifts in thinking, this paper provides a starting point for cladistic revisions that has been lacking in strombiod systematics in terms of re-evaluating the evolutionary relationships within the Stromboidea.

With the circumscription of *Dolomenini tribus nov.*, *Dolomenina subtribus nov.* and *Doxanderina subtribus nov.*, this study brings greater resolution to the internal structure of the Strombidae. Furthermore, this study demonstrated that, while the work of Abbott (1960; Jung and Abbott 1967) coalesced much of the historical taxonomy of Strombidae, the systematics contained within that work has led to a manifest limitation on the genus and species richness, and in particular, not yet recognized genera were ‘lost’ through a process of over-aggregation of similar taxa (Maxwell *et al.* 2018; Maxwell *et al.* 2019a). This has been resolved with the introduction of *Amabiliplicatus gen. nov.*, *Pacificus gen. nov.* and *Dominus gen. nov.*

ACKNOWLEDGEMENTS

Our warm thanks go out to Thierry Backeljau (Belgium, Royal Belgian Institute of Natural Sciences) for proofreading and the many suggestions for improvements of the paper. We value his efforts and advices improving the article. The advice to use DNA was however not our study.

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	Character State ¹																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<i>abbotti</i>	1	1	0	1	2	0	1	1	0	0	0	0	0	0	1	2	2	2	0	1	2	1	1
<i>apicatus</i>	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0	1	0	3	1	1
<i>athenius</i>	0	0	2	1	0	1	0	1	2	0	1	2	0	2	0	1	0	1	0	1	1	0	0
<i>campbelli</i>	1	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	0	1	0	1
<i>columba</i>	1	0	1	1	1	0	0	1	2	1	0	1	0	2	0	1	3	2	0	1	2	1	1
<i>dilatatus</i>	1	1	1	1	2	0	0	1	1	1	0	1	0	0	0	1	3	1	0	1	3	1	1
<i>entropi</i>	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1	0	3	1	1
<i>epidromis</i>	0	0	2	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	1	2	0	1
<i>hickeyi</i>	1	1	1	1	2	0	0	1	2	1	0	1	0	2	0	1	3	2	0	1	2	0	1
<i>japonicus</i>	1	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	2	1	1
<i>kleckhamae</i>	1	1	1	1	2	0	0	1	1	0	1	2	0	0	1	0	0	0	1	0	2	1	1
<i>labiosus</i>	1	1	1	1	2	0	1	1	0	0	0	0	2	0	1	0	2	1	0	1	2	1	1
<i>listeri</i>	1	0	1	0	0	0	0	0	1	0	2	1	0	1	0	0	0	2	0	1	0	0	0
<i>marginatum</i>	1	1	0	0	0	0	0	0	1	0	0	0	3	1	1	0	1	0	0	0	4	1	0
<i>minimus</i>	1	0	2	1	2	1	0	0	2	0	1	2	0	2	0	0	3	2	0	1	2	0	1
<i>orosminus</i>	1	1	1	1	2	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	3	1	0
<i>plicatus</i>	1	0	1	1	1	0	0	1	0	0	0	2	1	0	0	2	3	1	1	1	3	0	1
<i>pulchella</i>	1	0	1	1	1	0	0	1	2	1	0	2	0	1	0	1	3	2	0	1	3	0	1
<i>robustum</i>	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	2	3	0	0	0	1	0	0
<i>septimum</i>	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>sibbaldi</i>	1	0	0	0	1	0	0	1	0	0	0	1	1	0	1	1	1	2	1	1	2	0	1
<i>simanoki</i>	1	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	3	0	0	0	1	1	1
<i>sowerbyorum</i>	1	1	0	0	0	0	0	0	1	1	0	0	1	2	0	0	0	0	0	0	1	1	0
<i>succinctum</i>	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0
<i>swainsoni</i>	1	1	1	1	2	0	0	0	1	1	0	1	0	0	1	0	0	2	0	1	3	1	0
<i>vanikoriensis</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
<i>variabilis</i>	0	0	2	1	0	1	0	1	2	0	1	2	0	2	0	1	0	2	0	1	2	0	1
<i>vittatus</i>	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	0	2	0	0
<i>wienekei</i>	1	1	1	1	2	0	1	1	0	0	0	1	0	0	1	0	2	2	0	1	3	1	1
<i>yerburyi</i>	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	2	1	1	1	1	2	0	1

¹*Aperture* – (1) The texture of aperture: 0 - smooth; 1 - lirate. (2) Uniformity sculptural form of inner labrum: 0 - no change in ornamentation; 1 - variable ornamentation. (3) Marginal fold: 0 - absent; 1 - indistinct; 2 - distinct. (4) Lip edge callous: 0 - no callosity; 1 - calloused. (5) Texture of the columella: 0 - smooth/indistinct; 1 - lirate; 2 - lirate posteriorly and/or anteriorly. (6) Columella callosity prior to the formation of the anterior canal: 0 - uniform callosity; 1 - thickened basally. (7) The form of the columella: 0 - straight; 1 - sinusoidal. (8) Posterior sinus: 0 - long; 1 - short. (9) Posterior sinus lobes: 0 - open canal; 1 - sharp outer lobe; 2 - calloused outer lobe. (10) Shape of posterior sinus: 0 - straight/ moderately straight; 1 - strongly recurved. (11) Both sides of sinus well developed; 0 - not even; 1 - even; 2 - not developed. (12) Stromboidal notch and lobe: 0 - sinuous; 1 - moderately well formed; 2 - well formed. *Ventral Body Whorl* - (13) Sculpture of the shield: 0 - smooth; 1 - with axial ribbing; 2 - with thick axial folds; 3 - fine uniform striations. (14) Acute ridge left side of shield: 0 - absent; 1 - indistinct; 2 - distinct. (15) Shape of shoulder: 0 - angulate; 1 - rounded. (16) Sculpture of the shoulder: 0 - smooth/one or two small nodules; 1 - sculptured; 2 - with uniform nodules. (17) Shape of body whorl: 0 - fusiform; 1 - biconically acute; 2 - anteriorly cuneate; 3 - Quatrately fusiform. *Dorsal body whorl* - (18) Flange fold: 0 - absent; 1 - indistinct; 2 - distinct. (19) Flange: 0 - not stepped; 1 - uniformly stepped. (20) Cross sectional shape of flange: 0 - convex; 1 - straight. (21) Shoulder sculpture: 0 - smooth; 1 - with one or two faint knobs; 2 - distinct knobs; 3 - ribs; 4 - keeled. *Dorsal Teleoconch* - (22) Penultimate whorl spiral sculpture: 0 - smooth/ indistinct; 1 - with fine striations. (23) Penultimate whorl axial sculpture: 0 - smooth; 1 - uniformly plicate.

Table 1. Character states for typical representatives of each taxon.

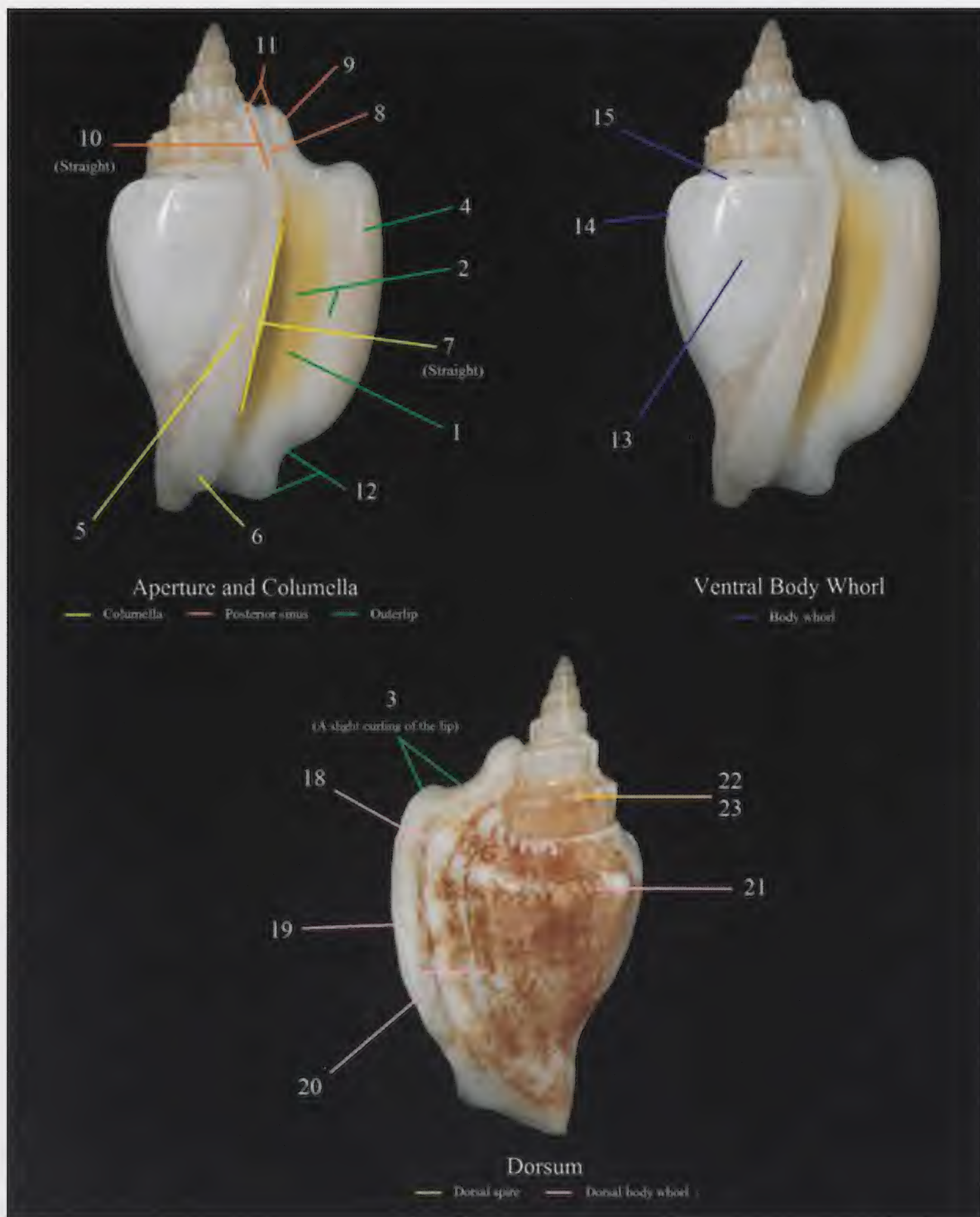


Figure 1. Morphological features used to determine character states - (1) The texture of aperture, (2) Uniformity sculptural shape of inner labrum, (3) Marginal fold, (4) Lip edge callous, (5) Texture of the columella, (6) Columella callosity prior to the formation of the anterior canal callosity, (7) The shape of the columella, (9) Posterior sinus lobes, (10) Shape of posterior sinus, (11) Both sides of sinus well developed, (12) Stromboidal notch and lobe, (13) Sculpture of the shield, (14) Acute ridge left side of shield, (15) Shape of shoulder, (16) Sculpture of the shoulder, (17) Shape of body whorl, (18) Flange fold, (19) Flange stepped at edge, (20) Cross sectional shape of flange, (21) Shoulder sculpture, (22) Penultimate whorl spiral sculpture, (23) Penultimate whorl axial sculpture.

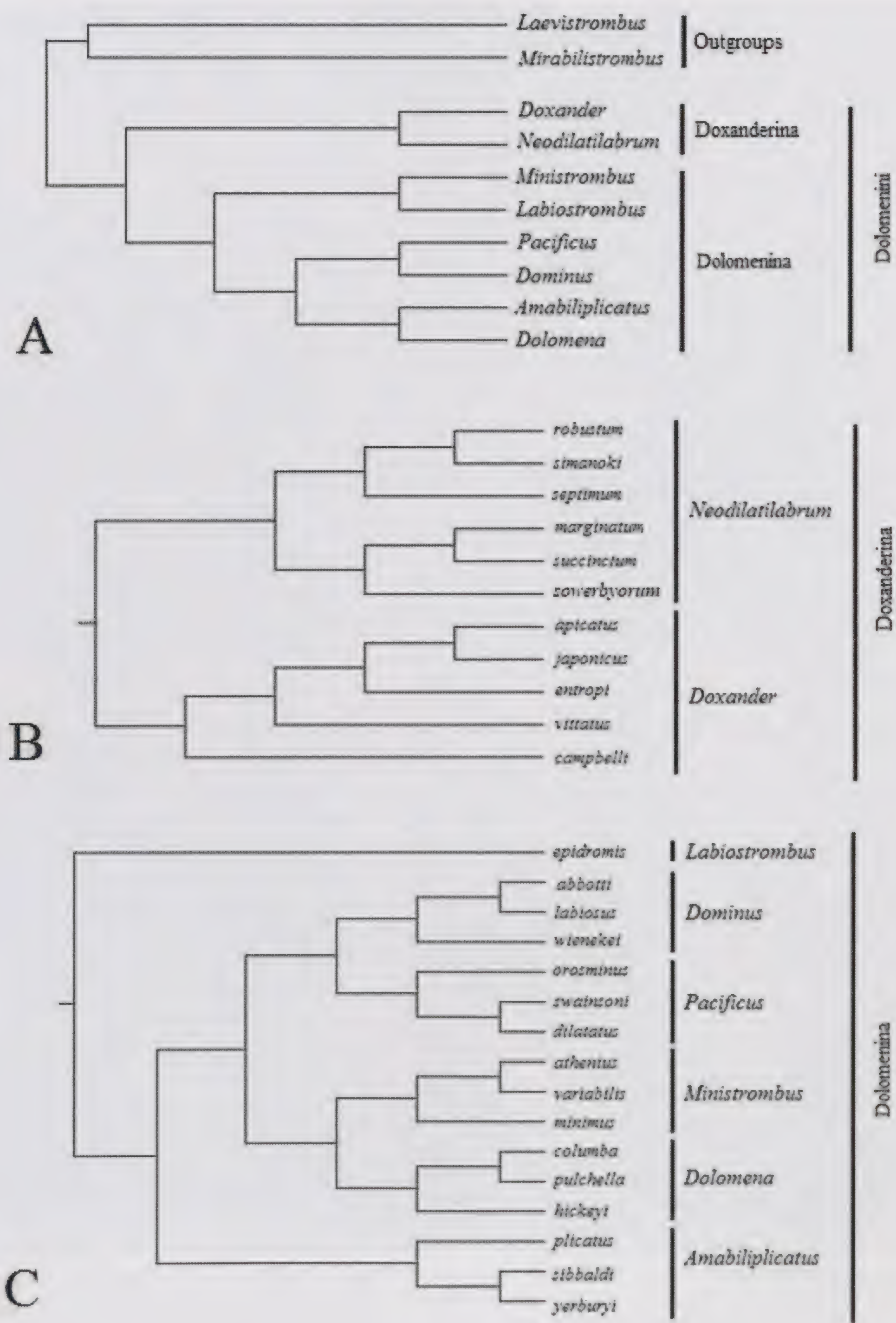


Figure 2. The revised phylogeny of Dolomenini tribus nov with the most parsimonious trees: A) The results of the first cladistic analysis using the type species for each genera resulting in two monophyletic groups, the Dolomenina subtribus nov. and Doxandrina subtribus nov., and the demonstration that *Mirabilistrombus* and *Laevistrombus* fall outside the Dolomenini tribus nov.; B and C) the resolution of the internal content of each of the two trees identified in the first analysis using all species extant contained within them.

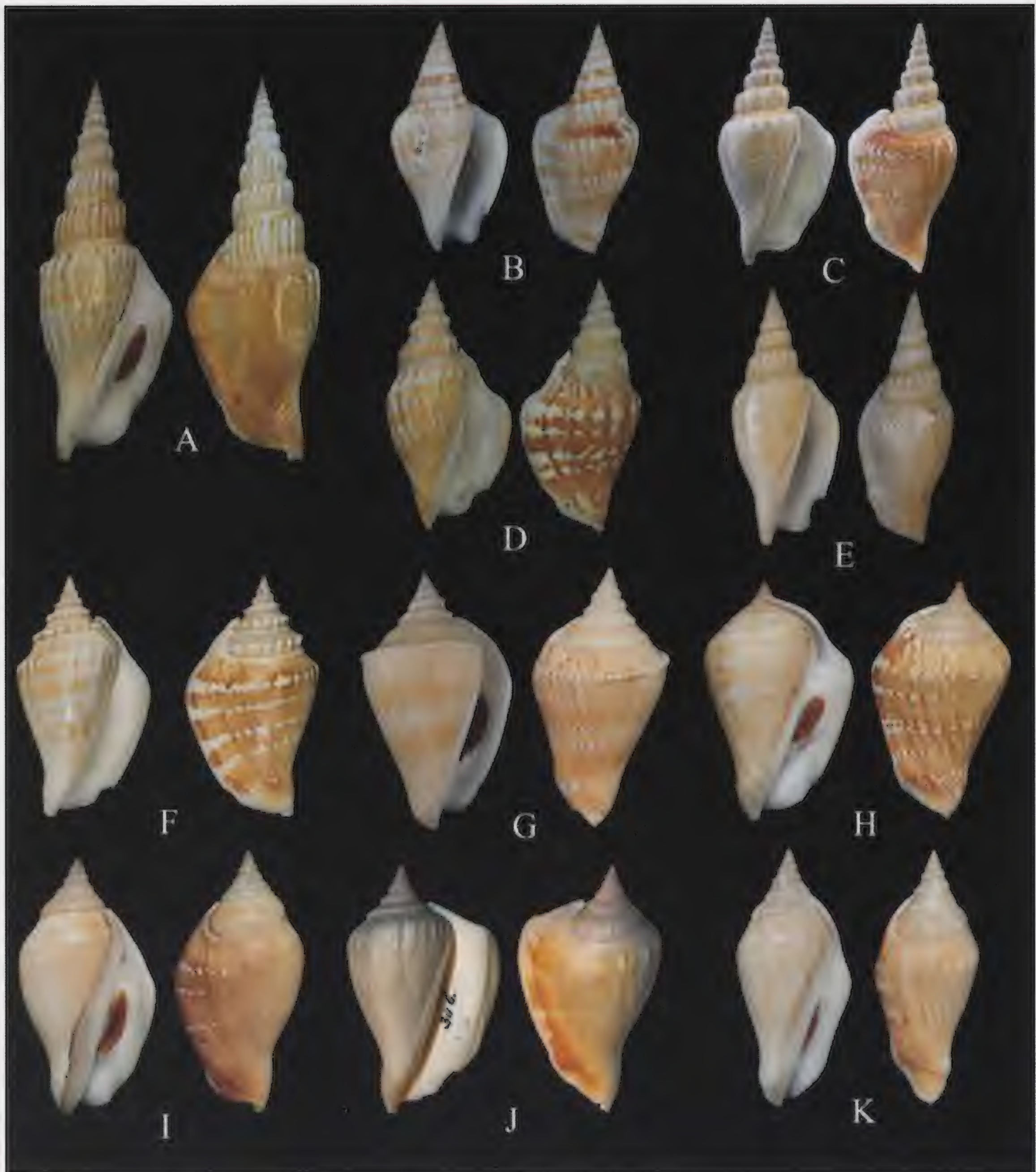


Figure 3. Iconography of *Doxanderina subtribus* nov.: *Doxander* Wenz, 1940 - A) *Doxander apicatus* (Man in't Veld and Visser, 1993), Quang Ngai, Vietnam, 92 mm, AMD STR0562; B) *Doxander campbelli* (Griffith and Pidgeon, 1834) Yirrkala, Gove, Northern Territory, Australia, 54 mm, SMC 13.026; C) *Doxander entropi* (Man in't Veld and Visser, 1993), Davao, Philippines, 82 mm, SMC 15.002; D) *Doxander japonicus* (Reeve, 1851), Honshu, Japan, 61 mm, AMD STR1058; E) *Doxander vittatus* (Linnaeus, 1758), Kurrumune Beach, Queensland, Australia, 61 mm, SMC 36.001. *Neodilatilabrum* Dekkers, 2008 – F) *Neodilatilabrum boucheti* (Thach, 2016) Khan Hoa Province, Vietnam, 45 mm, MNHN-IM-2000-30134 (= *Neodilatilabrum robustum* (Sowerby, 1875) fide Kronenberg *et al.* 2019). G) *Neodilatilabrum marginatum* (Linnaeus, 1758), Madras, India, 55 mm, SMC 66.002; H) *Neodilatilabrum sowerbyorum* (Visser and Man in 't Veld 2005), Okinawa, Japan, 48 mm, SMC 68.001; I) *Neodilatilabrum septimum* (Duclos, 1844), Balicasag Island, Philippines, 53 mm, SMC 69.002; J) *Neodilatilabrum simanoki* (Liverani, 2013), Sumatra, Indonesia, 54 mm, NCB-Naturalis RMNH MOL164040; K) *Neodilatilabrum succinctum* (Linnaeus, 1767), Madras, India, 53 mm, SMC 70.001.



Figure 4. Iconography of *Dolomenina subtribus nov.*: *Dolomena* Wenz, 1940 - A) *Dolomena columba* (Lamarck, 1822), Nacala Bay, Mozambique, 2010, 52 mm, SMC 60.001; B) *Dolomena hickeyi* (Willan, 2000), Dingo Beach, Queensland, 2006, 47 mm, SMC 57.001; C) *Dolomena pulchella* (Reeve, 1851), Cebu Island, Philippines, 1986, 33 mm, SMC 59.004. *Labiostrombus* Oostingh, 1925 - D) *Labiostrombus epidromis* (Linnaeus, 1771), Goeland Island, New Caledonia, 2015, 78 mm, SMC 40.008. *Ministrombus* Dekkers, 2008 - E) *Ministrombus athenius* (Duclos, 1844), Borneo, Indonesia, pre 1990, 34 mm, SMC 53.003; F) *Ministrombus minimus* (Linnaeus, 1771), Balicasag Island, Philippines, 2014, 33 mm, SMC 59.008; G) *Ministrombus variabilis* (Swainson, 1820), Dingal Island, Philippines, 2009, 55 mm, SMC 52.008. *Amabiliplicatus* gen. nov. - H) *Amabiliplicatus plicatus* (Röding, 1798), Egypt, Red Sea, 1962, 63 mm, SMC 61.003; I) *Amabiliplicatus sibbaldi* (Sowerby, 1842), Kerala, India, 2013, 36 mm, SMC 62.002; J) *Amabiliplicatus yerburyi* (Smith, 1891), trawled, Somalia, 2010, 45 mm, SMC 61.001.

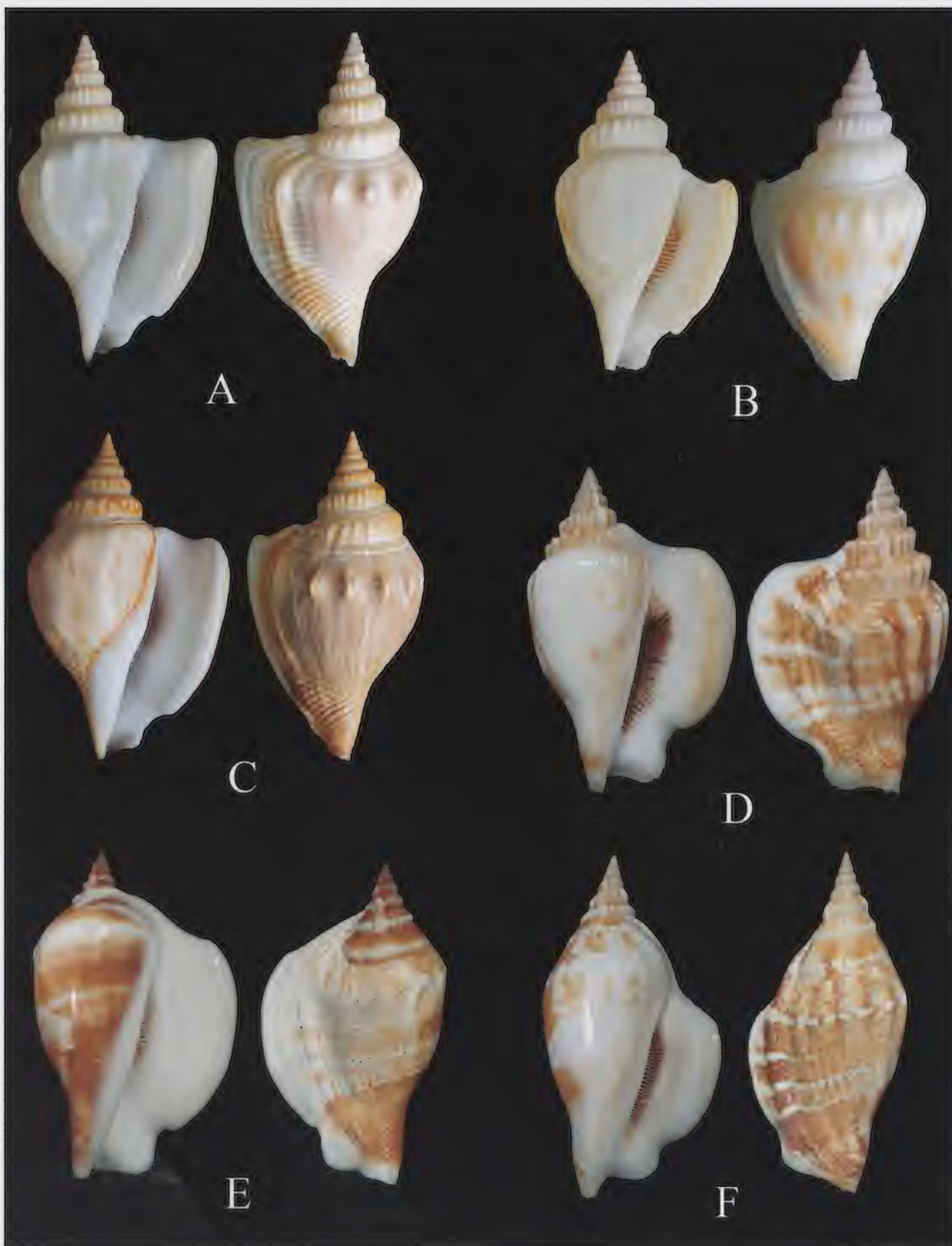


Figure 5. Iconography of *Dolomenina subtribus* nov.: *Dominus* gen. nov. - A) *Dominus abbotti* (Dekkers & Liverani, 2011), off Racha Island, Andaman Sea, 2005, 39 mm, SMC 65.001; B) *Dominus wienekei* (Wiersma & Monsecour, 2012), Rabaul, Papua New Guinea, 2000, 45 mm, SMC 64.001; C) *Dominus labiosus* (Wood, 1828), Tulear, Madagascar, 2010, 68 mm, SMC 63.001. *Pacificus* gen. nov. - D) *Pacificus dilatatus* (Swainson, 1821), Dingo Beach, Queensland, 2002, 40 mm, SMC 59.012; E) *Pacificus orosminus* (Duclos, 1844), Davao Island, Philippines, 2013, 53 mm, SMC 55.001; F) *Pacificus swainsoni* (Reeve, 1850), Vietnam, 2014, 71 mm, SMC 56.002.